Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

OBSERVATIONS ON THE HABITS AND NATURAL HISTORY OF AMPHITHOE LONGIMANA SMITH.

SAMUEL J. HOLMES.

In the present paper I have given the results of my observations made at Woods Holl, Mass., during the past summer on a species of amphipod, *Amphithoe longimana* Smith. Comparatively little is known of the habits of amphipods, and most of what is known has been collected from scattered and casual observations. There is a value in getting together all the facts that can be obtained concerning any one species of animal, so that they may be viewed in their *ensemble* and thus give us some idea of the general life of the creature. For this reason it was deemed best to devote the short time that could be given to the study of amphipod behavior mainly to the observation of a single species.

Throughout the paper I have used many terms which imply the existence in the animal of certain psychical states, such as hunger, fear, and courage, without intending to affirm that such psychical states really exist in the animal's consciousness, or even that the animal possesses consciousness at all. It is difficult to describe the behavior of an animal without the use of terms which have certain psychological connotations. Such terms are here used simply as a matter of convenience in describing actions simply as actions. The Crustacea may or may not be "Reflexmachinen," and Bethe and others may or may not be right in denying that they possess consciousness ; but, however this may be, descriptions of actions in psychological terms stand for certain peculiarities of conduct that could not otherwise be easily described, and if the sense in which such terms are used is understood, no confusion need result.

Amphithoe longimana may be obtained in large numbers from the eel pond near the laboratory by simply drawing a

net over the eel-grass. It is abundant during the summer months, a period when most of the other species of amphipods suffer a marked diminution in numbers. It is quite hardy, and may be kept alive for months in small glass dishes, if they are kept covered and the sea water kept fresh by a small piece of Ulva. Observations on this species were carried on for nearly three months. Specimens were kept isolated in small dishes and daily observations made and recorded. I was thus able to follow the histories of quite a number of individuals for a considerable period.

Specific Description.

Body slender. Eyes round. Lateral lobes of the head truncated in front. Antennules slender, about as long as the body, the second segment a little longer, but much more slender than the first; third segment from one-third to one-half the length of the second; flagellum much longer than the peduncle. Second antennae shorter than the first, but usually with a longer peduncle; last segment of the peduncle a little longer than the preceding one; flagellum shorter than the two preceding basal joints.

Second, third, and fourth epimera much longer vertically than wide; fifth epimeron about as long as the fourth, but broader and excavated at the upper posterior angle; lower margins of the epimera furnished with very short setae. Postero-lateral angles of the abdominal segments not acute.

First gnathopods in the male elongated, the first joint produced into a rounded lobe at the antero-distal angle; carpus narrow, nearly as long as the hand, and thickly setose on the posterior margin; hand very long and narrow, slightly incurved, and of nearly the same width throughout, although slightly widened near the base; lower margin setose; palm very short, transverse, and rounded at the outer angle; dactyl very large, dentate, and projecting far beyond the palm when closed. Second gnathopods much stouter than the first; first joint with a rounded lobe at the antero-distal angle; hand much broader and stouter than in the first pair; palm oblique, with a deep

sinus near the strongly produced outer angle; dactyl scarcely projecting beyond the palm.

In the female the gnathopods are much shorter and weaker than in the male; the hand in the first pair is less elongated, and the palm is more oblique and more broadly rounded at the outer angle. In the second pair the sinus in the palm is not so deep, and the outer angle not so prominent as in the male.

Peduncle of the first pair of pereopods rather slender, much longer than the rami, and reaching nearly to the tip of the peduncle of the second pair; inner ramus of the second pair of uropods about as long as the peduncle. Posterior pair of uropods with the rami scarcely half as long as the peduncle; rami subequal in length, the broader, more or less oval inner one with a short spine at the inner posterior angle and several setae on the transverse distal margin; outer ramus with the usual stout hooks. Length 6–9 mm.

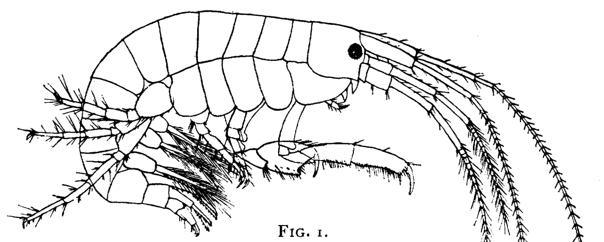

Fig. 1.

In the older specimens the antennae are relatively more elongated, and the hands of the male relatively longer and narrower. The eyes in the living specimens are red, but become black in specimens preserved in alcohol.

Habitat.

The range of this species as reported by Professor Smith is from Vineyard Sound to New Jersey, and it has been reported from Provincetown, Mass., by Richard Rathbun. It is not uncommon among the seaweed near the shore, and it has been taken at the surface in the vicinity of Woods Holl in the tow net. Its occurrence at the surface is probably due to its having been carried away from the shore by tide currents, as it has a strong tendency to keep among objects of shelter.

Its most favored habitat seems to be the eel-grass, where it finds a convenient substratum upon which to construct its nests. This species is much more common in the eel pond at Woods Holl than outside; the abundance of eel-grass and various algae and the quiet water being conditions which doubtless favor its perpetuation. It is not found on the muddy bottom and does not occur abundantly in the seaweeds near the bottom, but it may be obtained in quantity from the masses of eel-grass at the surface.

Enemies.

In common with most amphipods, Amphithoe is doubtless preyed upon by fishes, and it certainly affords one of the principal articles of food of the small but voracious jelly-fish Gonionemus. The latter form, however, owing to its unfortunate attractiveness to the zoölogists frequenting Woods Holl, is in danger of not continuing to be a very destructive enemy. It is very common to find Gonionemus with Amphithoe in its stomach. This crustacean falls an easy victim to its enemy, as it often makes surprisingly little effort to escape, owing possibly to a narcotizing effect of the poison of the nettling organs of its captor. I have seen an Amphithoe while swimming vigorously strike against the tentacles of the jelly-fish, suddenly stop, and remain almost perfectly quiet while it was being engulfed.

Food.

Amphithoe lives chiefly upon seaweed. The alimentary canal may usually be seen to contain numerous fragments of red or green algae. Pieces of Ulva that are kept in dishes containing these amphipods soon exhibit gnawed margins and, after some time, a marked diminution in size. I have often observed the process of feeding. The Ulva is gnawed directly by the mouth parts, without being previously torn away by the gnathopods. The quantity of algae eaten, judging by the amount of excrement voided, is very considerable. In order to ascertain how rapidly the excrement accumulated, a specimen with an abundance of Ulva was placed in a clean dish, and

it was found that one hundred and forty-six masses accumulated in twenty-four hours. These masses consisted almost entirely of broken-up cells of Ulva, the contents of which had been digested out. By making a very rough estimate based on the size of these masses, it was calculated that the amount of food eaten by the animal in twenty-four hours was about equal to one-tenth of its bulk.

Amphithoe is by no means a strict vegetarian, for it will devour animal food with great eagerness when it can be obtained. It is very fond of bits of flesh of almost any animal, not excluding that of its own species. When aware of the presence of food sufficiently near its nest to be seized without letting go its hold, it will dart out with a quick movement, grab the food with its gnathopods, and suddenly retract itself inside its domicile. When the food is brought in, it is held by the gnathopods while being devoured.

Movements.

Of the movements performed by Amphithoe, the beating of the pleopods is the most constant and uniform. Whether the animal is swimming, crawling, or lying quiet, the pleopods are continually engaged in their regular to and fro movement. The motion of these appendages while the animal is at rest serves to create a current of water past the gills in front, and thus aids in respiration. The abdomen, except during swimming, is held strongly flexed, forming a sinus, at the posterior end of which the bases of the pleopods are attached, the tips pointing forward. Small particles suspended in the water may be seen to be drawn in at the sides of this sinus and thrown out at the anterior end, thus indicating the course of the current.

The rhythm of the motion of the pleopods, like the respiratory movements of the higher vertebrates, goes on in a regular way as a rule, but may be checked by impulses from the higher nervous centers. When the animal changes its position, or executes any other decided movement, the pleopods may cease their action for a moment, but soon resume their regular beat

as before. Commonly during swimming the pleopods beat more rapidly, but this is not always the case. When the swimming ceases they drop back into their usual rhythm, whether faster or slower than before. In their motion the three pairs of pleopods act as a unit, keeping perfect time like well-trained oarsmen. If the abdomen be removed from the rest of the body, the pleopods, after a few spasmodic movements due to the shock of the operation, continue to beat rhythmically for several minutes; the three pairs all move with the same rhythm, though somewhat more slowly than before the operation. Moreover, if a single segment with its pair of appendages be isolated, the rhythmic motion of the appendages still goes on for some minutes, but gradually becomes slower and more irregular, until nothing but small twitches indicate the existence of irritability.

When the animal is in a vigorous condition the beat of the pleopods is rapid, but when the creature becomes weakened the beat becomes slower, yet as long as life lasts the pleopods continue their movements. The beat of the pleopods may still persist after the rest of the animal refuses to respond to any sort of stimulation.

The swimming of Amphithoe is mainly effected by the pleopods. The first impulse, however, is gained by the sudden extension of the abdomen, which gives the body a rapid forward movement. The abdomen is then held in an extended position and the pleopods, which then hang nearly at right angles to the body, serve to continue the forward motion. When swimming against the force of gravity the motion of the pleopods alone is not sufficient to keep the body going, and when the original impetus becomes exhausted the abdomen is bent forward and again suddenly extended, giving the animal a fresh start. The flexure of the abdomen before every stroke tends to draw the body backward. This, combined with the weight of the animal, causes ground to be lost between every stroke. Swimming towards the surface is therefore accomplished by a series of springs, between each of which the animal falls back more or less. While swimming horizontally the beating of the pleopods is all that is required to keep up the motion; specimens

may be seen swimming about for a considerable time without employing the abdomen.

Amphithoe has a decided disinclination for continuous swimming. Ordinarily it makes only short excursions from one place of concealment to another and generally stops upon meeting with the first solid object that comes in its way, although when situated where there is nothing to which it can lay hold it may swim for some time in a uniform manner. It may swim in various ways, on its side, or with either the dorsal or the ventral surface uppermost, and apparently gets along with about equal facility in any of these positions.

The beat of the pleopods tends to propel the body not in a straight line forward but in a circular course. The pleopods being on the ventral side tend to cause the body to veer around towards the dorsal side. When the body is held somewhat concave on the ventral side, as it often is, this tendency may be balanced or overcome by the tendency to move in circles in the opposite direction. Such a condition is analogous to a person rowing on one side of a boat with the rudder turned toward the side of the oar. By having the body extended to the right degree a straight course may be maintained. The direction of movement is often changed by the animal turning now on one side and now on the other. Circular movements in one direction are thus compensated for by circular movements in another as the animal turns over and a certain general direction of motion is maintained. When swimming on the back a nearly straight course is kept by rolling the body slightly to the one or the other side. Rolling is probably effected by the movements of the hinder pairs of thoracic legs. When the animal is swimming these legs project outward and backward. A downward stroke of these appendages on one side would push the same side of the body upward and roll it over toward the opposite side. In a larger species of amphipod, whose movements are not so exceedingly rapid as those of Amphithoe, I was able to see that the rolling of the body was effected in just this way. It is highly improbable that in Amphithoe a different method would be employed to produce the same result. However this may be, it is certain that

Amphithoe steers itself while swimming by altering the extension of the abdomen and by rolling from side to side. Lateral bendings of the body could not be seen to play a part in directing the swimming motions, although I have observed this method of steering employed by other amphipods.

Amphithoe longimana, like many other amphipods, is unable to walk over a plane surface. When out of water it is able to make indifferent progress by the characteristically amphipodan gliding movements produced by alternately flexing and extending the abdomen. It is utterly incapable of leaping like the sand fleas and some of their aquatic relatives. Owing to its compressed form, it is unable to maintain itself upright while out of water, or even in water, unless it has some object to which it can lay hold. In its characteristic habitat among the seaweed, Amphithoe crawls with considerable agility. The principal organs for crawling are the second antennae, the two pairs of gnathopods, the third and fourth pairs of pereopods, and to a certain extent the abdomen. The antennae are thrown over objects and flexed, thus tending to pull the body upward and forward. The gnathopods are used to seize objects in order to pull the body along. The two following pairs of appendages are employed much as the walking legs of insects, although they move in a nearly vertical plane. The abdomen assists in locomotion by being thrust forward beneath the body until the tip is hooked on to some irregularity of the surface over which the animal is moving when it is extended, thus giving the body a forward impulse. The movement recalls the leaping motion effected by the abdomen in the sand fleas. In fact, very similar motions are performed in both cases, but in Amphithoe the motions are much less rapid and energetic. The ambulatory movements of this species are never rapid, owing doubtless to the necessity for keeping the body from falling over on its side. The last three pairs of thoracic legs, although not used directly for locomotion, are indirectly of service in holding the body upright. These appendages, which are bent over the back and have their claws pointing forward, are used to hook on to objects and thus act as organs of support while progression is effected by the other appendages of the body.

Ordinarily Amphithoe lies in its nest, with the antennae protruding from the opening at the end. The lower pair of antennae are generally held motionless. The upper pair, however, are usually seen to be moving to and fro, sweeping about in almost every direction. Occasionally their motion is suddenly checked and they are held motionless for a time, but soon their movement is resumed. The significance of these movements will be discussed in a later section. The two pairs of gnathopods are used for a variety of purposes. Occasionally the antennae are bent downward and seized by the gnathopods and the flagella drawn through the space between the dactyl and the palm. The function of this act is probably to strip off any foreign bodies that may become attached to the antennae. The gnathopods are frequently employed to grab passing objects and to reach out and pull in bits of seaweed for the construction of the nest. They are used also for holding the food that the animal is eating and for carrying bits of food to the mouth, where they are taken by the maxillipeds. While not exercising any of their normal functions they may often be seen going through the motions of grasping, with nothing to grasp. This restless activity of the gnathopods seems to be nothing but the exercise of the grasping reflex called forth by some unknown stimulus and having no useful result. The act is performed in all degrees of completeness, from a definite grasping motion to a mere nervous twitch. The mouth parts perform many motions when the animal is not masticating food. These movements, which resemble the normal motions of mastication so far as could be observed, apparently have no functional significance. They take place in specimens kept for a considerable time in dishes in which there is nothing that could serve for food. Like the grasping actions, they are movements which are called forth without the normal exciting cause.

One of the most curious actions which Amphithoe performs is its reversal of position in the nest. If the antennae be somewhat roughly struck with a needle, or even if a threatening object suddenly appears close in front, the head and antennae will appear at the other end of the nest. As the nest is a tube

but little wider than the body of its occupant, no one who watches the operation can fail to have a feeling of admiration for the neatness and extreme quickness of this acrobatic feat. The animal executes this "about face" with such rapidity that it is only after watching the operation repeatedly that one can determine how it is effected. As the animal lies in its nest the abdomen is bent forward and the posterior pairs of thoracic legs are directed backward, their claws being usually hooked into the walls of the nest. When about to turn around, the abdomen is thrust forward, its terminal hooks caught in the nest; the tip of the abdomen, therefore, forms a fixed point, and the insertion of the thoracic legs forms another. The contraction of the legs would therefore pull the middle and anterior parts of the body backward. When the head is pulled back some distance, extension of the body occurs, forcing the anterior part of the body through to the other end of the nest. The head end being reversed, the abdomen is loosened and quickly flexed again under the body. The whole operation is completed in less than a second, and the animal may be made to repeat the performance several times in rapid succession.

Nests and Nest-Building.

The nests of Amphithoe are tubular structures which generally exceed somewhat the length of the animal. They are made of a web-like material which, under the microscope, may be seen to be a network of exceedingly fine threads. The nests are usually constructed among the branches of the red seaweeds or upon the leaves of eel-grass or the fronds of Ulva. When built upon Ulva the nest is generally located in a wrinkle or fold of the surface which affords a partial shelter. The nest is open at both ends and is of about the same diameter throughout. Foreign materials, such as bits of seaweed, are usually woven into the nest and greatly add to its efficiency as a means of concealment. Amphithoe frequently leaves its nest, but I could find no evidence that it would return to its own nest more readily than to any other; it will simply enter the first unoccupied nest that comes in its way. When established in

a nest Amphithoe is driven out only with difficulty. A member of its own species that approaches is grabbed at and usually driven off, and the creature appears to be on the alert to keep out all intruders. The approach of a more formidable-looking object causes the animal to retreat farther back into its nest. If the antennae are stroked with a needle, a sudden somersault will be executed and the head will appear at the other end of the nest. Then it usually requires quite a series of pokes to make the creature quit the nest entirely. The instinct to remain in the nest when danger threatens presents a marked contrast to the quickness with which flight is made when the animal is roaming free.

A new nest is constructed in a remarkably short time, often in less than a half hour. If a few specimens be placed in a dish of sea water containing a little seaweed, nests will be woven on the seaweed and on the lower surface of the dish, and in a short time the number of nests may greatly exceed the number of specimens. Those localities are chosen which give the animal a maximum of contact with solid objects. In dishes in which specimens were kept I have nearly always found several nests along the angle between the bottom and sides, although the seaweed kept in the dishes afforded localities better adapted for concealment. The choice of a spot for a nest is apparently largely a matter of thigmotaxis. When the animal remains in a spot for some time, the nest-building activities begin, and where contact with different sides of the body is secured, as between the branches of seaweed, in the wrinkle of an Ulva frond, or in the angles of a glass dish, it remains quiet. If Amphithoe is observed while constructing its nest, the first and second pairs of pereopods will be seen to be busily engaged in moving back and forth from point to point along the surface on which the web is being laid down. The first and second pereopods contain large glands which are connected with a duct which opens at the tip of the claw. The material for the web is secreted by these glands and probably hardens soon after its emergence, like the web of a spider. A very fine thread of web may frequently be seen passing out from the small opening at the tip of the claw. As the tip of

the claw touches one point after another, the web, as it is drawn out, is fastened to different places. By moving back and forth and rolling around during the weaving process, the animal constructs its tubular dwelling. Several specimens from which I clipped the claws from the first two pairs of pereopods were kept for several days and did not construct a single nest.

During the construction of the nest, Amphithoe will reach out and draw in bits of algae and other objects that lie near and incorporate them into its dwelling. In a few cases I have seen long pieces of algae bitten in two and used for this purpose. As Amphithoe lives largely on algae, this biting may not have had any special reference to nest-building, but may have been a manifestation of the ordinary reaction to food. In Microdeutopus, Smith has observed that the excrement of the animal is worked into the web; but in Amphithoe, whose nest-building habits seem to be very similar, no such process could be observed. The excrement is passed out of the nest, accumulations of it usually being observable near the two ends.

Moulting.

Amphithoe was found to shed its skin more often than was anticipated. Most of the specimens I kept isolated as long as a week moulted once, and out of four specimens in which I have records of the dates of two successive moults of the same individual the interval between moults in three cases was seven days, and in the other case eight days. These specimens were of the usual size. How rapidly moults occur in different periods of the life history of this species I cannot say.

The process of moulting in Amphithoe occurs in the same manner as has been described in other species of amphipods. The skin splits transversely along the line joining the head and thorax, and on either side of the thorax is a longitudinal split which occurs between the upper margins of the epimera and the lower margins of the thoracic rings. This split may extend along all the thoracic segments. The head and antennae are pulled backward out of their investment and the posterior part of the body is pulled out forwards, the old skin, after being

shed, remaining intact except at the lines just mentioned. The moulting process takes several minutes at least and is accompanied by considerable muscular effort to get out of the old skin.

In the several cases in which I observed the process, Amphithoe leaves its nest to divest itself of its skin, and I have never observed a moult in a nest but always some distance away. After moulting the animal is rather quiet and cannot easily be enticed from its nest by food. I have observed several cases in which death occurred during the moulting process. In one case moulting was not completed for several days. The specimen was observed August 17 with the head and tail ends drawn partly out of the old case. The next day the head and antennae were still not completely drawn out, but the rest of the skin was kicked off. On August 21 it was still in the same condition, the feeble beating of the pleopods giving evidence of failing strength. On the next day it died, the head and antennae still only partly extricated from their old covering. In several cases the antennae were observed to become broken off in the process of moulting, but I have seen no cases in which other appendages became lost in this way. The antennae are the appendages most liable to more or less complete loss from other causes, but owing to the rapidity with which these organs can regenerate this loss can produce only a temporary inconvenience. The cast-off skins are found sometimes on the bottom, and often floating on the surface of the water, and in a short time after they are shed become filled with swarms of protozoa.

The Seat of Smell.

Much has been written concerning the seat of the olfactory sense in the Crustacea, but most opinions on the subject have been based on morphological instead of experimental evidence. The work of May and Bethe affords good evidence that in the decapod Crustacea the seat of the olfactory sense, or, as Bethe prefers to call it, of chemoreception, is in the first antennae, as analogy with the insects would lead one to suspect. The first antennae are not, however, according to Bethe, the only seat

of chemoreception. In Carcinus the removal of the first antennae as far as the first basal segment is followed by a marked diminution of the power of reaction to chemical substances in the water. A Carcinus when the eyes are blackened over will find pieces of food when placed at some distance, by the sense of smell. When the first antennae are removed at the first basal segment, Bethe found that food may be placed as near as 10 cm. to the animal without calling forth any efforts to obtain it. When the food is brought close to the mouth or close behind the animal without contact with the body, it is seized and eaten. The first antennae, therefore, while they may be the main, are not the sole source of the reception of olfactory stimuli.

My own observations on Amphithoe led me, before becoming acquainted with Bethe's results, to infer a double seat of the sense of smell. In Amphithoe, as in Carcinus, the first antennae seem to be the most important olfactory organs. While the animal is at rest in its nest the antennules are kept swaying to and fro in different directions, as if they were being employed to explore the surroundings. If a small bit of flesh is held on a needle or in a fine pair of pinchers and carefully brought near the animal, the antennae check their random movements and make one or more strokes in the direction of the bit of flesh; often the antennae are held for some time in the direction of the object. On bringing the flesh nearer, the animal may be seen to adjust itself in the nest for a sudden spring, and if the flesh is sufficiently near to be touched by the antennules the amphipod makes a sudden dart from the nest, seizes the object, and draws quickly back again, never letting go its hold, however, of the nest. The animal as a rule readily distinguishes between the contact of flesh and that of a body not serviceable for food. Only rarely does touching the antennule with a needle call the animal forth from the nest. It may be deceived more often if, when excited by the presence of meat near by, one of its antennules be touched with a needle; then it may dart out towards the needle and even seize it. But the animal responds much more surely, as I have found by repeated experiments, when the antennules come in

contact with the food itself, even when the animal is excited by the presence of food in its vicinity. The darting forth, therefore, is apparently caused, not merely by a tactile stimulation, but by a chemical stimulus from the food. The antennae are delicate tactile organs, and tactile stimuli may assist in calling forth the actions which result in the seizing of food, but tactile stimulation alone generally fails to accomplish this result.

After Amphithoe has made a meal of fleshy diet it becomes quite indifferent to the presence of that kind of food in its vicinity and no longer darts forth to grab bits of flesh brought in contact with its antennules. Different individuals present very different degrees of eagerness for animal food, owing doubtless to varying intervals of time since their last repast.

Sight has probably little to do with the food reactions of the animal. When the head is completely withdrawn in the nest the animals often give signs of perceiving food and dart after it when brought in contact with the antennules. In many cases the nest is so opaque that the animal cannot see through it with any distinctness, and under these circumstances, when the head was entirely withdrawn into the nest, I have often brought bits of meat so they would be touched by the antennules only when they were strongly bent backwards. Although the meat was out of sight, the amphipod would dart out, bend backwards, and seize the morsel. If the desired object is out of reach of the antennules, the amphipod will not spring for it, although it may be seen to make ready to do so. It will not go to the length of leaving the nest to seize food, even if its conduct betrays evidence of keen hunger. An object near enough to be struck by the swaying of the antennules is sufficiently near to be seized by the animal without letting go its hold of the nest. It is a noticeable feature of the species of Amphithoe and related genera that the antennules are, roughly speaking, of about the length of the body. This feature is not improbably correlated with the similar tube-dwelling habits of these forms, the length of the antennules gauging the length of a safe and successful spring.

The effect of removing the antennules of Amphithoe is greatly to lessen responsiveness to olfactory stimuli. The

shock of the operation has a very temporary effect, for in a few hours the animals behave with their usual activity. Meat brought in contact with the second antennae is generally not seized. This, however, is not always the case, for in several instances I have found that contact with the second antennae causes the grasping reflex. I was inclined at first to attribute a certain olfactory sensibility to the second antennae, but I found later that the animal reacts about as well to olfactory stimuli when both antennae are removed as when the second alone remain. In specimens with both antennae removed near the base, leaving only the first joint of the peduncle of each pair, there was no reaction to food placed in what would have been within easy reach of the antennae before their removal. If a piece of meat is placed about 2 mm. from the mouth of the amphipod, it is generally allowed to remain untouched for several seconds and then suddenly seized and eaten. The morsel is seized by the gnathopods and at the same time bitten at with the mouth parts. The reaction is not an immediate one, such as is brought about by contact of the antennules with food. It appears to be necessary for the food to remain awhile in close proximity to the animal before its edible nature is perceived; when this occurs the seizing takes place quickly enough. I have tried to induce the animals to take bits of substance of the general appearance of fragments of meat and brought very close to the mouth parts, but they are apparently able to distinguish, before any contact with the object occurs, whether or not it is of an edible nature. It is true that Amphithoe often grasps objects that lie near by, pulls them back, and incorporates them into the structure of its nest, and it might be inferred that the seizing of meat lying close to its mouth by a specimen with both antennae removed is an expression of the nest-building instinct to seize any small object within reach for building material. The reactions in the two cases, which I have observed many times, differ. An object used for the construction of the nest is reached for and pulled back to the nest and not as a rule brought in contact with the mouth. A bit of meat is grabbed at and bitten at in the same act. This difference in reaction and the fact that

the animals seize bits of meat when they cannot be induced to pay attention to other objects of similar appearance convinced me that the reaction to food was caused by chemical stimulation from diffusing substances in the water.

Removal of the second pair of antennae, the first being left intact, was not found to exert any marked influence upon reactions to chemical stimuli. The second antennae may transmit olfactory stimuli; it would be difficult to prove they do not in a certain degree, but the evidence obtained does not justify us in attributing to them this function. When, after removal of the first antennae, Amphithoe responds when food is brought in contact with the second antennae, the reaction may be due to the animal becoming aware of the presence of food through some other organ, contact with the antennae indicating that the food is sufficiently near to be seized. In other words, the reaction may be due to purely tactile stimulation, the animal being keyed to this reaction by the excitement of olfactory stimuli from some other organ. What other organ, or organs, may serve to transmit olfactory stimuli is uncertain. This has not been determined in the decapod Crustacea, which afford the only other instance in which a double seat of the olfactory sense has been suspected, or in fact in which, so far as I am aware, any experimental evidence has been adduced as to any location of this function at all. It seems probable that some of the mouth parts have some olfactory function, as they afford the most obviously appropriate location for such a sense. Owing to its small size, Amphithoe is not a favorable form in which to decide this question, and the attempt to do so was not made.

Color and Color Changes.

One cannot but be struck, when examining a number of specimens of this species, with the marked differences in color presented by different individuals. Some are bright green, like the bright green seaweeds; others may be nearly colorless; a few are of a light blue green tint, and many range from a light to a dark reddish-brown. The same individual may take on, at different times, all these varieties of coloration. The color

differences are produced by the variation of five elements: (1), the color of the chitinous integument; (2), the color of the blood and tissues; (3), the contents of the alimentary canal; (4), the color of the sex glands; (5), the pigment cells. The first of these factors is, perhaps, the least important and is not subject to great variation. The exoskeleton over most of the surface of the body is colorless; on the antennae it is marked with transverse reddish-brown bands which give the light reddish-brown annulations of these organs. This color is seen as distinctly in the shed skin as in the living animal.

The color of the tissues and blood is subject to great variation. The green color of Amphithoe, or the blue green tint when it occurs, is due to some coloring matter that is uniformly diffused throughout the animal. In some specimens there is a sufficient amount present to give the animal a brilliant emerald green, but many may be found in which not the slightest trace of green coloration could be detected. This green color may be seen to undergo marked changes in intensity if individuals be watched for several days. The blue color is much rarer. One specimen in which this blue coloration was strongly marked was kept under observation for several days. After five days most of the blue color had disappeared, the green becoming more nearly like the typical green of other forms. After six days the green was not to be distinguished from the ordinary type; the green color then gradually became fainter, and on the ninth day the tissues were whitish, scarcely a trace of green being visible. During all this time the specimen ate abundantly of green algae, judging from the amount of excrement consisting of Ulva cells that accumulated in the dish.

The contents of the alimentary canal influence to a considerable extent the general color effect produced by the animal when seen by the naked eye. If they consist largely of green Ulva, they tend to give the animal a greenish appearance. If the Ulva has been subjected some time to the action of the digestive juices and become a yellowish color, it tends to give the animal a corresponding yellowish aspect. Light becoming colored by passing through the alimentary canal is reflected and re-reflected in the tissues and tends to make them appear

a corresponding color. I have several times cut off parts of the body to see if their color might not have been due to this cause; but whatever effect this factor may have it is certain that the green color of the blood and tissues is not entirely caused in this way as it may easily be observed in the isolated appendages. The part played by the sexual glands in the coloration of this species varies greatly owing to the variation in the size of these organs.

It is to the pigment cells that the most marked changes of color are due. These cells are of two kinds, — reddish-brown pigment cells, and cells with a pale green pigment. The latter play an insignificant part in the coloration of the animal, as they are pale in color and few in number, there being often not more than a dozen on the entire surface of the body. The pale green color appears most clearly in transmitted light; in reflected light they are of a silvery hue. Their size is about the same as the largest cells with red pigment. Like the latter, they are very richly branched, but were not seen to undergo much variation in the distribution of their pigment. They are mainly confined to the epimera, being usually situated near the lower margin.

The most important elements in determining the color changes are the reddish-brown pigment spots. These spots are scattered all over the body and are found also on most of the appendages, especially towards the proximal end. When extended the pigment spots are large and very richly branched, forming most beautiful objects when seen under the microscope. When fully contracted these spots assume the form of round dots, and all stages of expansion may be seen in different specimens, or even in the same specimen, between the most contracted and the most expanded state. There are a few large spots near the lower edges of the epimera that are generally found in an expanded condition. Even when most of the spots over the surface of the body are contracted, these few spots, which may be not more than a dozen on each side, are usually conspicuously large. This circumstance affords a convenient means of distinguishing *Amphithoe longimana* at a glance from other species of the same genus.

The pigment spots of Amphithoe apparently contain but one kind of pigment. The whole system of chromatophores is much less complicated than that which Gamble and Keeble[1] found in *Hippolyte varians*, and the power of sympathetic color changes in relation to surrounding objects much less perfectly developed. Amphithoe may be said to adapt its color to its environment, but in only a rather rough way compared with the remarkable protective color changes of Hippolyte. Specimens taken from the eel-grass are very apt to be of a greenish color, and specimens taken from among masses of red seaweed are usually colored somewhat like their environment. While on the eel-grass, they are usually exposed to the light and the pigment spots are in a contracted condition. This allows the green color of the tissues to be seen, and the animal has, consequently, a greenish aspect. In the masses of red seaweed the animal is usually more shaded and the pigment spots become expanded, giving the animal a reddish tint which helps to conceal it in its environment. Moreover the alimentary canal in specimens found in the red seaweed often contains a greater or less quantity of this alga, and this also helps to color the animal in a protective manner. So far as the green color of the tissues is concerned there appears to be no difference between the animals from different habitats. The change from green to reddish, or the reverse, completes the range of adaptive color variations in this species so far as they are induced by changes in the environment. And this kind of color change is the one best adapted to afford protection to the species in its usual habitat.

The pigment spots of Amphithoe change very slowly; it generally requires some hours to effect a change from the expanded to the contracted condition. It was found by several experiments that exposure to bright light causes the pigment spots to contract, while specimens that have been kept in the dark for several hours generally have the pigment spots much expanded.

[1] *Quart. Journ. Micr. Sci.*, 1900.

Sexual Habits.

Concerning the sexual habits of Amphithoe I have little to add beyond what is known among other amphipods. The male carries the female about for a considerable period and maintains his hold against efforts to dislodge him with great pertinacity. The instinct to retain hold of the female is sufficient to overcome all fear, and it is difficult to separate the male without injury. The posterior part of the body may be cut off, and yet the anterior portion retains its hold of the female as long as sufficient vitality remains. Ordinarily the male retains his hold of the female by hooking the claws of his pereopods beneath the edges of the epimera. The gnathopods are not generally employed for this purpose, but are called into use when a sudden disturbance renders the hold of the male insecure. The female remains remarkably passive when carried about by the male. Her body is usually held quite strongly flexed and the male does the swimming for both, the female being transported as so much dead weight. While carried by the male the female seems much less responsive to stimuli than when free. When poked by a needle she often makes little motion, but the more alert male is generally aware of the disturbance and carries her away from the seat of annoyance.

The Disposal of Excrement.

In its natural position Amphithoe lies so that the excrement that is voided would be deposited in the nest. Yet the excrement is never found in the nest but at some distance from either end. At first I supposed that it was carried out by the current of water produced by the movement of the pleopods, but, after watching the animal, I noticed that when excrement was extruded the abdomen was bent forward and the gnathopods reached back and seized the mass as it was ejected from the intestine, and passed it out of the front end of the nest. This act was observed three or four times, but whether it is always performed when excrement is extruded I cannot state. In one individual lying outside a nest on the bottom of a glass

dish I noticed that when excrement was passed the abdomen was bent forward and the mass seized by the gnathopods and passed forward, just as it is when the animal is in the nest. There was of course no use in seizing the excrement under the circumstances, but the act was performed in the usual instinctive way nevertheless.

Timidity and Pugnacity.

Specimens of Amphithoe are very ready to attack other amphipods that come near and drive them away. The animals appear to be on the alert to prevent any other individual from gaining access to the nest, — so much so that they very frequently spring out at a passing amphipod and bite at it in what appears to be a particularly vicious and hateful manner. The individual attacked does not, so far as I have observed, attempt any defense but precipitately flees from the spot. Anything that properly could be called a fight is never engaged in; a passing nip with the gnathopods, or bite with the jaws, is all that seems to occur in the nature of hostilities.

While ready to dispute the entrance of another amphipod from in front, Amphithoe generally quickly flees from its nest when an intruder enters from behind. One often sees the occupants of nests routed out by others entering in this way, and I have seen one individual that was expelled by another entering behind it swim around, enter the other end of the nest, and drive out the intruder. Courage in Amphithoe depends in great measure on whether the attack is made from in front or behind.

Outside the nest Amphithoe is very timid. It does not attack its fellows except by giving an occasional nip when accidentally colliding with them, and it flees quickly when disturbed. It can very rarely be induced to seize meat, however hungry it may be, and however carefully the food be presented. Even when in the nest, care has to be taken in offering the animal food lest it be alarmed by one's movements. This alarm is manifested by withdrawing a short distance in the nest. When an animal to which meat is presented withdraws in this way, I find that it is useless to attempt to

induce it to take food for several minutes, until its fright wears away. Experience in feeding these animals soon enables one to tell whether or not they have become frightened by your actions.

So far as my observations go they indicate that Amphithoe has very little true pugnacity. It does not engage in a conflict in order to overcome an adversary, as many decapod Crustaceans do; it fights only in self-defense. The attacks on other amphipods passing by the nest are simply measures to keep out unwelcome visitors. Had not these forms the instinct to keep the nest to themselves, several individuals would often crowd into the same nest much to their mutual inconvenience.

Phototaxis.

Amphithoe, like most of the aquatic Gammaridea, is negatively phototactic. The specimens experimented with were placed in an elongated, rectangular dish contained in a box open at one end and above and blackened on the inside. When placed near a window, either in direct sunlight or so that rays of diffuse daylight fell obliquely into the dish, the animals would swim towards the end of the dish farthest from the source of light. When the dish was turned about, they swam back again to the other end. In lamplight they may be driven alternately from one end to the other by moving the lamp back and forth to opposite ends of the dish. The endeavor was made to make Amphithoe positively phototactic by altering the temperature and concentration of the sea water, but only negative results were obtained. The animals remain negative until the water is heated to about 90° Fahr., when little responsiveness to light remains. Further heating causes heat rigor to supervene. Increase of temperature may be carried to the point of producing death without changing the direction of the phototactic movements. It is not probable that cooling the water below the normal temperature would alter the phototactic response. Decrease of temperature, other things equal, tends to give rise to negative phototaxis in Orchestia, and increase of temperature has the effect of making this form more positive.

Raising the temperature has the effect of making *Gammarus mucronatus* positively phototactic, but an increase of only a few degrees beyond the point where its phototaxis changes produces heat rigor. Possibly Amphithoe might be rendered positively phototactic could it endure a somewhat higher temperature.

Neither increasing nor decreasing the concentration of the sea water was found to effect a change in the direction of phototaxis. A more extended account of phototaxis in the Amphipoda will appear in another paper.

Thigmotaxis.

The tendency of Amphithoe to keep in contact with solid objects is one of the most conspicuous features of its behavior. This tendency is apparently one of the fundamental instincts of the group, as it is exhibited very strongly by most of the Amphipoda. When placed among branched seaweeds, Amphithoe stops only after it works its way among the branches where there is contact on several sides of the body. In Ulva it comes to rest in a fold of the frond. When placed in a glass dish containing nothing but sea water, it swims about restlessly and eventually comes to lie quiet in the angle between the bottom and side. The instinct to crawl into an empty nest is an expression of the same tendency. Were it not for its thigmotaxis, the whole conduct of the animal would be very different from what it is. Many other instincts, like the nest-building instinct and the instincts associated with it, are built upon this fundamental reaction as a foundation. It does not seem improbable that the instinct of the female to remain perfectly quiet while carried about by the male, and even the strong propensity of the male to seize and retain hold of the female, may be but modified and specialized forms of thigmotaxis. Given variations of responsiveness to contact in different parts of the body, and variations in the manner in which the responsiveness is exhibited, we would have the means by which thigmotaxis might be modified by natural selection into more specialized forms of behavior. If the origin of the various

forms of amphipod behavior could be traced, it would be found, I believe, that thigmotaxis is the mother of many instincts.

The Instincts of the Young.

When the young of Amphithoe quit the maternal brood pouch, they have a quite different appearance from the adult. They are whitish in color, with only a very few pigment spots, located for the most part on the epimera, each epimeron containing often but one spot. These pigment cells are of a greenish-gray color and apparently have none of the reddish-brown pigment which is found in those of the adult. By reflected light they have a light greenish-silvery appearance much like the large light green cells of the adult, but they are very much smaller and much less branched. The head is relatively large, but the eyes are small and red and composed of only six ocelli, one of which is in the center surrounded by five others. The number of ocelli, therefore, increases very greatly as the animal grows older. Both pairs of antennae are short, the flagella of the first pair consisting of four joints and those of the second pair of but three.

The young when first hatched are in a feeble condition and are carried about for a few days in the brood chamber of the mother. Before they are hatched one can easily see the beating of the heart and the peristaltic movements of the intestine. Shortly before their emergence the young may be observed flexing and extending the body in the effort to break the shell. In one case I removed a lot of eggs from the brood pouch of the mother while they were hatching. Those that had not yet emerged were very vigorous in their movements within the shell. When hatched they were unable to swim, and their movements were irregular and little cöordinated. The next day a few had died; the others could swim feebly, but none well, and if they became caught in the film at the surface of the water they were unable to overcome the surface tension and get free. In another case I removed from the brood pouch of a female several young that had been hatched only for a short time, as they were feeble and scarcely able to swim.

The swimmerets, however, beat rapidly, and the maxillipeds and gnathopods were in constant motion. The antennules were moved more than the antennae, but their movements were more jerky and irregular than in the adult. The next day several others came out of the brood pouch of the mother of their own accord. They were a little more active than those that had been removed the day before and exhibited apparently a faint negative phototaxis. They had been out only a short time when they began constructing nests. These nests were the same in shape as those formed by the adult, and the behavior of the young in relation to the nest was almost exactly like that of the older individuals. One of these young impaled on a needle was presented to one of the same brood lying in its nest. At first the animal gave signs of timidity and withdrew further into its nest. After some waiting the animal emerged a little and began waving its antennules in the usual manner. When they touched the food the creature darted out quickly, seized it, dragged it back, and proceeded to devour it at leisure. Apparently, it is only one or two days after hatching that the young get effective control of their movements, and they probably remain at least that long in the maternal brood pouch. When they are sufficiently active to make their exit they are equipped for the business of life. It was a matter of some surprise to observe how perfectly endowed the young are with the instincts of the parent forms. Their behavior in almost every respect seems exactly like that of the adults. The nest-building, movements within the nest, such as waving the antennules, retraction, reversal of position, springing out after food, jumping after passers-by, signs of timidity, as well as the general behavior outside the nest, are all carried on just as in individuals many times their size.

Regeneration.

No attempt was made to study the power of regeneration in Amphithoe, but it may be worth while to record a few observations that were made incidentally on the regeneration of the antennae. The antennae were removed in several specimens

while studying the reactions of the animal to olfactory stimuli, and it was noticed that the regeneration of these appendages took place with considerable rapidity. Several observations were also made on specimens in which the antennae were found to have been accidentally lost. In a specimen (Fig. 2) observed August 13 the left antennule had been removed at the end of the second joint, and the right one at the end of the first. Of the second antennae the left member was off at the end of the fourth joint, which had a small, apparently regenerated knob at the end, and the right was gone at the end of the third and had a black tip. On August 16 the specimen moulted and the antennae appeared as follows: The right antennule had regenerated the last two joints of the peduncle and a flagellum of twelve joints; the left antennule also had completed its peduncle and regenerated a flagellum of seven joints, two of which were partially constricted in the middle and may have later become separated into two joints each. The second antennae had both completed their peduncles, the fifth joint in the right one being somewhat longer than in the left. The left antenna as a whole, however, was longer than the right, and its flagellum consisted of nine joints, while that of the right was composed of seven. How long the antennae had been injured when the observation was first made I cannot state, but it was certainly since the previous moult, so these appendages were probably regenerated in not much over a week and possibly in a less time. In another specimen first observed August 13 the left antennule was gone at the end of the second joint, and the right one at the middle of the second joint. The left second antenna was off near the end of the fourth joint, and the right one at the end of the third. After moulting, which occurred on August 14 or 15, the right antennule had a completed peduncle and a flagellum of six joints; the left antennule did not regenerate. Each of the second antennae had a complete peduncle, and the left one had a flagellum

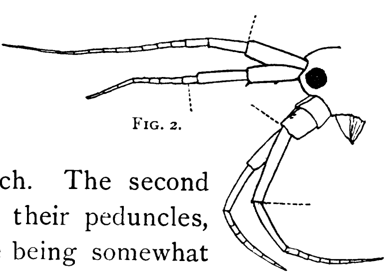

Fig. 2.

of three joints and a minute terminal fourth joint; the right one had a flagellum of four joints.

The Effect of Cutting the Animal in Two.

It has been found in many of the lower animals that, after removal of the posterior part of the body, the anterior portion manifests little signs of pain and acts as if no injury had been received. Many interesting cases of this kind have been collected by Dr. Norman in his paper entitled "Do the Reactions of the Lower Animals against Injury indicate Pain Sensations?" [1]

In order to see how the removal of the posterior part of the body affects the behavior of Amphithoe, I cut the animal in two just behind the third thoracic segment. In the posterior piece the thoracic legs moved but little, but the pleopods kept up their rhythmical beating for fully a half hour. The anterior part of the animal apparently suffered little discomfort, since, after the operation, it behaved much as if forming a part of the whole organism. The animal lay moving its antennules to and fro and making the usual movements of its gnathopods, just as an uninjured specimen would do. A piece of meat was brought near so that it was struck by the movements of the antennules; it was first swept a little nearer by the second antennae, and then quickly grabbed by the gnathopods, drawn in, and eaten, although the food could pass through only the small part of the alimentary canal that remained. Since this reaction in the normal animal is readily prevented by fear, and only occurs when the animal is hungry, it is somewhat surprising to find it performed after such a serious injury as the loss of the posterior half or more of the body. The animal behaves in such an apparently normal manner after this operation that it would seem as if the loss was scarcely felt. Owing to the loss of the posterior part of the body, many of the actions of the animal are naturally impeded or prevented. It cannot, for instance, get meat except when it is placed quite near, as it is unable to make its accustomed spring out of the nest. But in general,

[1] *Am. Journ. Phys.* Vol. iii, p. 271. 1900.

so far as the actions of the animal are modified, they are affected rather by the loss of certain organs than by any shock to the central nervous system. The loss of blood consequent upon the operation soon leads to weakness and finally death. Were it not for the profuse bleeding that occurs, the separated halves of the body could probably be kept alive for a long period.

University of Michigan,
Ann Arbor, Mich.